



# Response of eastern white pine and associated foliar, blister rust, canker and root rot pathogens to climate change<sup>☆</sup>

Stephen A. Wyka<sup>a,\*</sup>, Isabel A. Munck<sup>b</sup>, Nicholas J. Braze<sup>c</sup>, Kirk D. Broders<sup>a</sup>

<sup>a</sup> Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, USA

<sup>b</sup> Forest Health Protection, USDA Forest Service, 271 Mast Road, Durham, NH 03824, USA

<sup>c</sup> UMass Extension, Center for Agriculture, Food and the Environment, University of Massachusetts, Amherst, MA 01002, USA



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## ABSTRACT

Climate model predictions for the northeastern U.S. forecast a warmer and wetter climate, which favors the survival, reproduction and dispersal of foliar diseases of eastern white pine, collectively called White Pine Needle Damage (WPND). Foliar diseases cause defoliation of white pine, leading to growth reductions, canopy dieback and predisposing trees to other pathogens and insects. This situation is very similar to other conifer foliar diseases, such as *Dothistroma* needle blight (DNB) in British Columbia and Swiss needle cast (SNC) in Oregon, where the climate is also becoming warmer and wetter. The purpose of this review is to summarize recent WPND findings of the impact climate change, particularly increased spring precipitation and annual warming has on the emergence of this disease complex. These findings will then be related to what is currently known about climatic factors affecting DNB and SNC and their role as native foliar pathogens affecting their natural forest ecosystems. We also discuss other eastern white pine diseases such as blister rust, cankers, and root rots in relation to climate change.

## 1. Introduction

As the climate continues to change, researchers remain focused on understanding how these variations in environmental conditions influence pathogen migration, incidence, and severity (Garrett et al., 2006). This task is particularly complex in natural forest settings due to the long-lived nature of trees and the relatively short generation time of pathogens, thus providing pathogens the ability of a faster genetic response and quicker adaptability to new climate conditions (Brasier, 2001; Sturrock et al., 2011; Burdon et al., 2012; Gray et al., 2013). Changes in climate have been shown to directly affect forest pathogens' ability to persist in an ecosystem through: increased growth, increased rates of dispersal, expanded geographic ranges, and increased overwintering survival (Dukes et al., 2009).

Over the past decade, eastern white pine (*Pinus strobus* L.) has been suffering from a severe and destructive needle blight outbreak in northeastern North America which has been caused by recent shifts in the regions climate (Munck et al., 2011; Wyka et al., 2017a). Many foliar pathogens causing needle diseases are sensitive to precipitation and humidity and exhibit increased rates of reproduction, spread, and infection under moist conditions (Sturrock et al., 2011; Harvell et al.,

2002). The favorable effects of warming temperatures, for foliar species such as *Mycosphaerella pini* (Rostr.) could be offset by the negative effect of decreased summer precipitation, resulting in an overall decrease of the pathogen population over time (Desprez-Loustau et al., 2007). Dry summers are predicted to occur in the northeastern region of the United States (Campbell et al., 2011), leading to drought stress which could predispose trees to *Caliciopsis pinea* and *Diplodia sapinea*, two of the more damaging forest pathogens in the region. Although, drier summers have little effect on the spread and survivability of WPND as this emergent disease complex is favored by spring/early summer precipitation, which is expected to increase in this region (Campbell et al., 2011).

The impacts of climate change on forested ecosystems are already being felt at a greater frequency and the severity of biotic attacks and climate extremes—as well as interactions between biotic and climate stressors—have contributed to increased tree mortality rates worldwide (McDowell et al., 2011; Woods et al., 2017). Defoliation by pathogens and environmental stress can limit a tree's ability to take up water and nutrients, which can affect forest productivity and carbon stocks (Hicke et al., 2012). Much recent attention has focused on the interaction between drought and disease on tree health given the many regions of

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\* Corresponding author.

E-mail address: [Stephenwyka@gmail.com](mailto:Stephenwyka@gmail.com) (S.A. Wyka).

the world predicted to experience hotter and drier future conditions. However, in some areas, including the northeastern U.S., climate change forecasts predict a wetter and warmer climate (Hayhoe et al., 2007), which will most certainly favor foliar pathogens, as has been recently documented for WPND in the Northeast (Wyka et al., 2017a,b), Dothistroma needle blight (DNB) in British Columbia (Woods et al., 2016), and Swiss needle cast (SNC) in parts of Oregon (Agne et al., 2018). Despite the complexity of understanding climate-pathogen interactions, it is still prudent to continue to investigate potential disease risks in forest ecosystems that are experiencing increases in both temperature and precipitation. This is especially true when the affected host, eastern white pine, is not only an essential economic lumber resource but a crucial ecological component of the forests of northeastern United States and eastern Canada.

## 2. Climate change in the natural range of eastern white pine

### 2.1. What are the future climate predictions for this region?

Climate change projections for the northeastern USA include increases in both temperature and precipitation, resulting in an overall warmer and wetter climate for the region (Hayhoe et al., 2007). A continuing trend towards warmer and wetter condition could be supported by long-term measurements at the Hubbard Brook Experimental Forest in New Hampshire, which show increased temperature and precipitation (Campbell et al., 2011). In addition, the northeastern U.S. has experienced above average precipitation and average to above average temperatures from 2003 to 2014, including six years that were in the top 10% for precipitation (with 2011 being the wettest on record), and four years in the top 10% for temperature (NOAA, National Climatic Data Center, 2015). While this data represents annual precipitations, seasonal weather data analyses predict increases in precipitation in every season but summer (Campbell et al., 2011). Increases in temperature are expected to lengthen the growing season, and thus, the length of time that foliar pathogens can be active. Drier and hotter summers could result in water deficits that would lead to the development of drought stress in plants (Hayhoe et al., 2007). Increases in temperature are also expected within winter months, which will likely improve overwintering survival of forest pathogens. However, previous research of foliar diseases of conifer forests indicates that increased spring precipitation is the most influential climatic factor favoring reproduction and dispersal of foliar pathogens and thus disease severity such as Dothistroma needle blight (DNB) (Woods et al., 2016), Swiss needle cast (SNC) (Manter et al., 2005), and white pine needle damage (WPND) (Wyka et al., 2017a).

### 2.2. How might climatic changes affect foliar, blister rust, root, and stem canker pathogens?

Shifting environmental conditions can lead to interacting stresses that may predispose eastern white pine to decline (Manion, 1981). These changes may result in increased exposure to abiotic stresses that directly impact white pine, such as drought, cold/freeze injury and airborne pollutants (Benoit et al., 1982; McLaughlin et al., 1982). Weakened trees are more susceptible to attack from opportunistic fungal pathogens, of which there are many associated with eastern white pine in the northeast (Hepting, 1971; Sinclair and Lyon, 2005). Shifting climate patterns may favor the pathogens of eastern white pine, by increasing the time that specific environmental conditions (e.g. a temperature and humidity range, duration of free moisture on the surface of tissues, etc.) that are necessary for spore production and dispersal exist. For example, increases in precipitation from May through July in the northeast are resulting in increased levels of spore production and dispersal of foliar pathogens when eastern white pines are most susceptible to infection (Wyka et al., 2017b). While drought is often associated with forest declines (Allen et al., 2010), the chronic

effects of needle blight on eastern white pine due to increased early season precipitation may prove to be the most important climate-induced shift.

Eastern white pine needle damage (WPND) has become a serious issue throughout the range of white pine over the past decade, with four fungal pathogens identified as having a significant role in the epidemic (Broders et al., 2015; Wyka and Broders, 2016). Foliar diseases are rarely lethal to forest and landscape trees, but they create a chronic and compounding stress as needles are killed (Hansen and Lewis, 1997). The repeated defoliation of conifers can result in reduced photosynthetic capacity, decreased growth rates, increased susceptibility to environmental stresses and fewer resources to combat opportunistic insect pests and fungal pathogens (Maguire et al., 2002). Opportunistic pathogens considered to be secondary in importance to white pine, such as *Lophodermium* spp. and *Diplodia sapinea* (Fr.) Fuckel, may benefit from weakened and stressed trees and could become more prominent members of the needle blight complex.

Increased precipitation and high humidity is also expected to favor sporulation and spore dispersal of *Cronartium ribicola* J.C. Fisch., Hedwigia: 182 (1872), the causal agent of white pine blister rust (WPBR) (Dukes et al., 2009). In the Northern Rockies, where WPBR has caused devastating mortality to native pines, wave years of blister rust have been associated with maritime weather conditions favorable to reproduction of the pathogen in the northwestern portions of the region (Geils et al., 2010; Mielke, 1943; Smith and Hoffman, 2000). In contrast to the Intermountain West, although WPBR is widespread and chronic in the Northeast, the disease incidence is limited to < 10% of trees affected in stands where it occurs (Lombard and Bofinger, 1999; Ostrofsky et al., 1988). The relatively low WPBR incidence in the Northeast, has been attributed to the effective program to eradicate the alternate host: *Ribes* spp. (Benedict, 1981; Geils et al., 2010; Ostrofsky et al., 1988). In Maine, Ostrofsky et al. (Ostrofsky et al., 1988) investigated WPBR incidence across WPBR hazard zones developed by Charlton (Charlton, 1963) for the Northeast based on climatic conditions favorable to the reproduction and dispersal of the pathogen. Contrary to expectations, WPBR incidence was not related to hazard zones. White pine blister rust incidence was related to past *Ribes* eradication efforts, and thus, the authors concluded that the *Ribes* eradication program was effective in controlling WPBR in Maine (Ostrofsky et al., 1988).

Root, butt and trunk rot fungi of eastern white pine are abundant and yet often overlooked because symptoms and signs of infection are cryptic or confused with other stresses. *Armillaria ostoyae* (Romagn.) and *A. mellea* (Vahl), regarded as two of the most virulent species of *Armillaria* (Morrison, 2004), were the most commonly isolated species from declining and dead white pines in Massachusetts (Brazee and Wick, 2011). Further, the incidence of *Armillaria* was significantly higher on white pines in the suppressed and intermediate crown classes, illustrating the preference of the fungus for low vigor trees. *Armillaria* has been reported to be particularly virulent to regenerating white pines when large inoculum reservoirs, such as hardwood stumps, are present nearby (Hepting, 1971). In managed stands of white pine, serious losses of merchantable timber have been reported due to *Armillaria* (Silverborg and Gilbertson, 1962). Additional root and butt rot pathogens that regularly attack eastern white pine include *Phaeolus schweinitzii* (Fr.) and *Heterobasidion irregulare* (Garbelotto & Orosina). White pines in both natural stands and plantations are affected, but especially trees growing in dense, low vigor plantations (Spaulding, 1952) and those where thinning operations have facilitated spread of *H. irregulare* (Hepting, 1971). By far, the most important trunk rot pathogen of white pine is *Porodaedalea pini* s.l. (Brot.) (Wendel and Smith, 1990). While fruiting bodies are generally uncommon and mostly observed on trees over 100-years-old (White, 1953; Silverborg and Gilbertson, 1962), young trees in natural and managed stands can also be infected (Hepting, 1971). A study of trunk rot pathogens of white pine in eastern Canada revealed that among the 13 wood-decaying



pathogens that were isolated, *P. pini* s.l. accounted for 90% of the volume loss present (White, 1953). Additional investigation on trunk rot pathogens of white pine revealed a similar result, with *P. pini* s.l. responsible for > 75% of all volume loss (Basham and Morawski, 1964). Greater numbers of stressed and weakened trees coupled with increasing temperatures that extend the growing season for these fungi could allow root, butt and trunk rot fungi to assume a greater role in tree decline and mortality (Dukes et al., 2009).

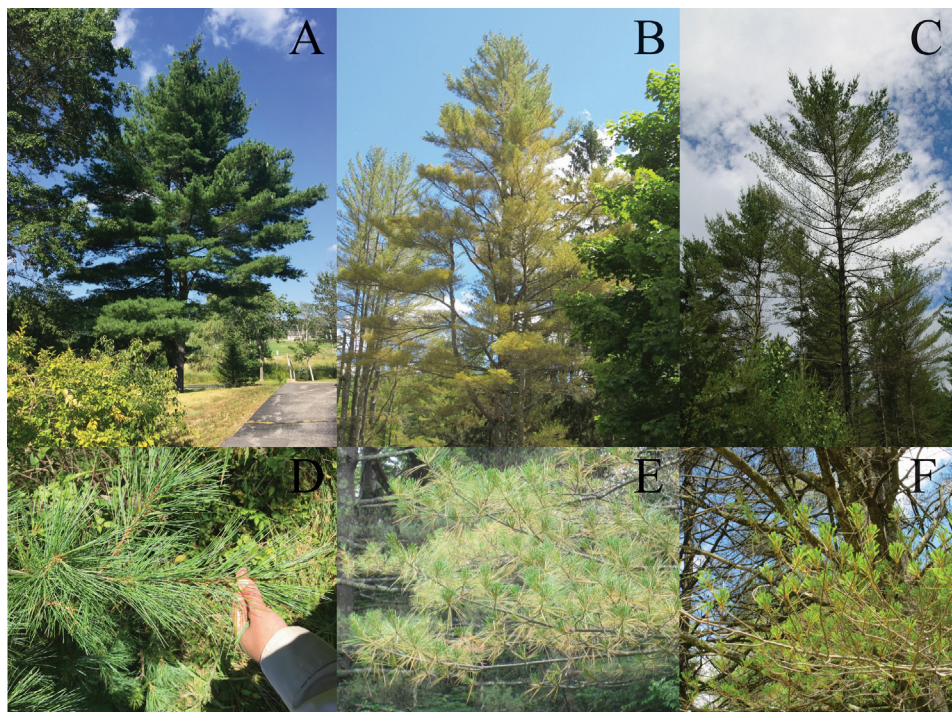
Tree decline and death is often the result of the combined effects of environmental stress, insect pests and disease-causing pathogens (Manion, 1981). Additionally, because eastern white pine is a disturbance-dependent tree species that is only mid-tolerant of shade, competition-induced stress, such as a lack of water and sunlight, can be an important factor in the mortality of understory trees (Yeaton, 1978). It is therefore important to better understand how climate change will influence, through predisposition and direct interaction, the assemblage of native and introduced insect pests and pathogens of white pine. For example, (Shaw and Toes, 1977) found that growth reductions and decline of *Pinus radiata* (D. Don) were greater in stands affected by both *Dothistroma pini* (Hulbary) and *Armillaria*. This comprehensive, landscape-level view has been applied to better understand the interacting effects of drought and attack by secondary pests and pathogens on the decline of quaking aspen in Colorado (Marchetti et al., 2011). Caliciopsis canker of white pine, caused by the native pathogen *Caliciopsis pinea* (Peck.), has become more abundant and destructive to white pine in New England in recent years (Munck et al., 2015a). There are numerous, additional secondary stem and branch cankering fungi that will opportunistically colonize weakened eastern white pines, such as *Phomopsis*, *Cytospora* and *Pestalotiopsis*, among others (Sinclair and Lyon, 2005). The interactions between foliar pathogens, root, butt and trunk rot fungi and stem and branch cankering fungi will be important to elucidate if, as predicted, the decline and mortality of eastern white pines continues.

### 3. White pine needle damage; why here, why now?

Since 2010, eastern white pines in the northeastern U.S. have been under attack by a foliar disease complex, white pine needle damage

(WPND), consisting of four fungal pathogens *Lophophacidium dooksii* (Corlett & Shoemaker), *Bifusella linearis* (Peck.) Höhn, *Lecanosticta acicola* (Thüm) Syd., and *Septorioides strobi* (Wyka & Broders) (Fig. 1). Prior to the current WPND outbreak, these foliar fungi were not historically associated with widespread disease of mature eastern white pines in this region. Both *L. dooksii* and *B. linearis* have been present in the northeast since the early 1900s, however, reports indicate that disease occurred on < 0.1% of eastern white pine stands throughout this region (Merrill et al., 1996; Wenner and Merrill, 1998; Minter and Millar, 1984). Similar findings were made from eastern white pine stands in Atlantic Canada from 1950 to 1996 (Harrison, 2009). While *L. acicola* was previously reported causing damage of eastern white pine in West Virginia and North Carolina in the 1950s (Boyce, 1959), in Wisconsin and Pennsylvania in 1991 (Stanosz et al., 1991), and was recorded once out of 871 collections from the Forest Disease Survey in Atlantic Canada from 1950 to 1996 (Harrison, 2009), it was only first reported in the northeastern U.S. in 2006 (Munck et al., 2011). Furthermore, *S. strobi*, a novel foliar pathogen of eastern white pine in the northeast, was discovered in 2012 and was the first report of a fungus in the *Septorioides* genus in North America (Wyka and Broders, 2016). Moreover, Forest Watch participants, who have studied the impact of ozone on eastern white pine over the past 25 years, did not observe WPND induced defoliation until 2010 (Rock and Carlson, 2013).

As wetter and warmer climates have occurred over the past decade in the northeastern U.S., these optimum conditions are likely to promote foliar disease caused by fungal pathogens as has been seen for WPND (Wyka et al., 2017a). Above-average precipitation over this period of time not only led to increased rates of disease during the wettest years, but has also resulted in a large buildup of inoculum that has facilitated high levels of disease during years of average or below-average precipitation (e.g. during the 2010 and 2016 growing seasons; NRCC, 2017). Based on aerial surveys in 2010 (Fig. 2), these fungi were responsible for 24,369 ha of damage to white pine forests in Maine (Frament et al., 2011), while in 2012 they caused damage to 4898 and 1496 ha of white pine forests in New Hampshire and Vermont, respectively (Frament *per. comm.*). While WPND-infested white pine trees are generally capable of recovering from a single defoliation event, in 2014 the first cases of mortality in eastern white pine due to repeated



**Fig. 1.** Photos of mature eastern white pine: (A) healthy white pine Durham, NH taken in August 2017, (B) white pine with WPND chlorosis Bethel, ME taken in June 2014, (C) WPND induced defoliation Bethel, ME taken in June 2014, (D) close up of healthy branch showing current, 2nd and 3rd year needles Pittsburgh, PA taken in July 2017 (E) close up of WPND chlorosis of 2nd year needles and green emerging needles Mohawk Trail State Park, MA taken in June 2013. (F) close up of WPND induced defoliation of 2nd year needles and green emerging needles Bethel, ME taken in June 2014. Photo credits: Bill Ostrofsky (C) & Isabel Munck (A, B, C-F).



Fig. 2. Aerial photo of mature eastern white pine stand exhibiting chlorosis induced by WPNP in central NH taken in June 2015. Photo credit: Ryan Hanavan.

WPNP-induced defoliations were observed. These findings largely agree with reports of *L. acicola* on other *Pinus* species within the U.S. (Siggers, 1944; Skilling and Nicholls, 1974; Phelps et al., 1978; Huang et al., 1995; Heimann et al., 1997), but it appears the eastern white pine is more tolerant of the pathogen (Wyka et al., 2017b). Due to changes in global climate and first reported case of WPNP-induced mortality, concerns over WPNP has expanded to an international level as important pine growing regions including Canada and Europe have been affected (Chandelier et al., 1994; Hintsteiner et al., 2012; Jankovsky et al., 2009). Given the rise in reports of these four foliar pathogens, two of which were not reported in the northeastern U.S. prior to 2006, two studies were conducted to help understand what regional shifts could have allowed an increase in the populations of *L. dooskii* and *B. linearis*, as well as an establishment of both *L. acicola* and *S. strobi* in the regions eastern white pine population.

As with all phytopathological diseases, researchers needed to consider all aspects of the disease triangle to determine which factor (host, environment, or pathogen) is largely responsible for the observed outbreaks. Wyka et al. (2017a) hypothesized that changes in seasonal temperatures and precipitation within the northeastern U.S. drove the current WPNP epidemic. They provided support for this hypothesis through expanding field sampling to construct a more detailed distribution of WPNP throughout the region and determining which environmental factors are driving the emergence and spread of WPNP.

### 3.1. Host abundance

From 2011 to 2014, 210 trees of all age classes from 70 eastern white pines stands ranging from natural wetland to dry steep slopes to urban and rural areas were sampled across the northeastern U.S. needles were assessed for presence or absence of the four fungal pathogens and distributions were mapped on a host layer risk map comprised of stands of > 50% eastern white pine basal area. Results showed that neither individual nor co-occurring combinations of these fungal species were found to exhibit a dominating presence (> 50%) in any particular state or region (Wyka et al., 2017a). All four foliar diseases were dispersed throughout the region and generally occurred in areas where host layer maps indicated > 50% basal area, however, all species were also found in areas where eastern white pine represented < 50% basal area. The host layer map revealed that the majority of the northeastern U.S. is heavily forested with eastern white pine, which could be due to increases in abundance at lower elevations in NH from long histories of heavy disturbance (Vadeboncoeur et al., 2012). Woods et al. (2005) indicated that increases in host abundance influenced the epidemic proportions of Dothistroma needle blight (*Dothistroma*

*septosporum* (Dorog. Morelet.) on lodgepole pine (*Pinus contorta* var. *latifolia* Engelman) in British Columbia, Canada. The high density of eastern white pine in the northeastern U.S. is not a recent establishment as both Maine and New Hampshire were the top two producers of white pine lumber since the 1940s (Betts, 1954). While Vadeboncoeur et al. (2012) indicated that some areas in the region are experiencing an increase in eastern white pine abundance due to long term history of heavy disturbance, some believe that the losses of eastern white pine from original forests are not being fully compensated for by its increase in abandoned pastures or agricultural areas (Abrams, 2001; Thompson et al., 2013). In central New England, there has been a gradual decline in the proportion of white pine due in part to reduce logging activity and the devastating effects of the 1938 hurricane, when many white pine-dominated stands were destroyed (Foster, 1992). Eastern white pine is still abundant in the region, but in comparison to pre-European settlement white pine has become more abundant in some areas and less abundant in others. Overall, it appears that the host density for eastern white pine has not increased. Therefore, the current WPNP epidemic was not incited by a recent increase in host abundance, but the already high host abundance favors the potential distribution of these four foliar pathogens as all are dispersed through rain splash (Wyka et al., 2017a).

### 3.2. Changing environment

To determine the role of climate on the defoliation severity of WPNP, Wyka et al. (2017a) utilized four years of annual defoliation severity data from (2012–2015) from eight established long-term monitoring plots (Munck et al., 2011). Temperature and precipitation data for each of the eight monitoring plots were collected from land-based stations maintained by the National Oceanic and Atmospheric Administration (NOAA/National Climatic Data Center). A total of thirty-four climatic variables were used to model the defoliation events from the climatic conditions of the previous year (1-year lag time). Results indicated that cumulative precipitation during May, June, and July was positively correlated with, and determined to be the best individual climatic predictor for the following year's WPNP defoliation event (Wyka et al., 2017a). The best overall model was a 5-factor regression model that included cumulative summer and spring precipitation, cumulative May precipitation, average max winter temperature, and average minimum March temperature. This 5-factor model was confirmed as the best predictor model when 2016 defoliation data, from the eight monitoring plots, became available after the study.

### 3.3. The pathogen

While WPNP is considered a disease complex, during the course of multiple year of field sampling it was determined that *L. acicola* is the primary pathogen associated with the majority of the mid-summer discoloration and defoliation (Broders et al., 2015; Wyka et al., 2017a). To provide further support for the observed association between *L. acicola* and defoliation, a field based spore dispersal study was performed (Wyka et al., 2017b) to better understand how climatic variables affect the abundance and distance of spore dispersal of *L. acicola* and impact needle defoliation through the summer and autumn. Results indicated that *L. acicola* spore release occurred primarily from May through July with peak release in June, corresponding to site-wide defoliation of the 2nd and 3rd year needles Wyka et al. (2017b). Climatic modeling indicated that relative humidity and occurrence of rainfall positively influenced spore abundance. Additionally, spore abundance was observed to be significantly higher in 2015 than 2014. When compared to litterfall measurements, the low abundance of *L. acicola* spores in 2014 resulted in low infection potential which was reflected in the decrease of the June 2015 litterfall collection. The increase of spores seen in 2015 was the result of frequent rainfall and



consistently high relative humidity prior to the June 2015 defoliation event. Consequently, this higher spore abundance observed in 2015 resulted in a higher infection potential that was reflected in increased litterfall in the June 2016 collection (Wyka et al., 2017b). These results largely agree with the findings of Wyka et al. (2017a) which showed that the amount of precipitation in May – July has a positive impact on WPND defoliation severity in the following year.

The high-density of eastern white pine within the northeastern U.S., coupled with increases in annual temperature and precipitation, has provided ideal condition for *L. dooksii*, *B. linearis*, *L. acicola*, and *S. strobi* to become emergent and reach epidemic proportions within this region. These factors have allowed for increased inoculum loads of both *L. dooksii* and *B. linearis* which have been present within the region since the early 1900s (Wenner and Merrill, 1998) and also has provided necessary ecological requirements for the rapid establishment and dispersal of *S. strobi* and *L. acicola* throughout the region. Defoliations due to WPND will likely increase in the coming years as current climate scenarios for the northeastern U.S. predict increases in annual spring and early summer precipitation and warmer winter temperatures (Frumhoff et al., 2007; Campbell et al., 2010, 2011). It appears eastern white pines will continue to experience annual premature defoliations, of their 2nd and 3rd year needles (Fig. 2), leaving behind weakened trees during the summer that are more susceptible to other abiotic and biotic stresses.

#### 4. Preparing for the next emerging tree pathogen. What have we learned from other systems?

##### 4.1. Similarities between global expansion of *Dothistroma* needle blight and white pine needle damage

While WPND in the northeastern U.S. is likely the result of a complex of needle pathogens, the predominant pathogen associated with the most significant defoliation is *Lecanosticta acicola* (Broders et al., 2015). There has been an increase in the number of reports of brown spot needle blight, caused by *L. acicola*, from around the world, which resembles the global expansion of *Dothistroma* needle blight (DNB) over 50 years ago (Gibson, 1972). DNB is one of the most economically important foliar pathogens of *Pinus* species worldwide (Bradshaw, 2004). The disease is caused by two species of *Dothistroma*, *D. septosporum* and *D. pini*, which are morphologically similar and generally require molecular identification to discriminate the two species (Barnes et al., 2004). For the sake of brevity, we will refer to DNB as being caused by both pathogens as the symptoms are very similar. Outbreaks of DNB have been observed around the world beginning in the 1950s and 1960s, but started to become more frequent and in more locations through the 1990s (Woods et al., 2016). Given the phylogenetic similarity of *D. septosporum* and *D. pini* to *Lecanosticta acicola*, and the abundance of epidemiological information recently reviewed by Woods et al. (2016), DNB may serve as a good proxy for the potential global expansion and increase in severity caused by brown spot and the impact climate change may have on accelerating this process.

*Dothistroma pini*, *D. septosporum* and *L. acicola* are all members of the Mycosphaerellaceae (Videira et al., 2017) and have similar disease cycles and epidemiology. There have been a few recent reports of the epidemiology (Wyka et al., 2017b) and effect of climate change on *L. acicola* (Wyka et al., 2017a) and these both focused on the disease in the northeastern U.S. However, the disease is known to be present throughout North and South America, but rarely reaches epidemic proportions in these regions. The same could have been said of DNB prior to 1950. Since then, the global incidence and severity of DNB has increased steadily in regions where it was established and has expanded into new regions and new hosts (Drenkhan et al., 2014). The rapid response of DNB to favorable weather conditions make it plausible that changes in disease severity are likely due to changes in climate (Woods et al., 2016). Within the literature there are a number of similarities

between the epidemiology of DNB and brown spot needle blight. Spring and summer rainfall, and in particular peaks in spring and above-average summer rainfall are associated with outbreaks of both DNB (Bulman et al., 2013; Gibson, 1972; Woods et al., 2005) and brown spot (Wyka et al., 2017b). Increased summer precipitation has also been associated with the development of DNB in the new host species, *Abies concolor* (Gordon) A. Murray, in Estonia (Drenkhan et al., 2014). While *L. acicola* can infect several species of *Pinus*, it is unclear if increased precipitation in the eastern U.S. and Canada will lead to host expansion. The increased precipitation over the last decade in the northeastern U.S. is also associated the emergence of *Septorioides strobi*, a new fungal species associated with the defoliation of *P. strobus*. Further investigation is needed in order to validate this connection. Increases in summer temperature had a limited effect on WPND (Wyka et al., 2017a), while it did increase the presence of DNB (Desprez-Loustau et al., 2007; Fabre et al., 2011), but rainfall was still a better predictor of disease severity.

Given the importance of temperature and precipitation and the vast literature on DNB from countries around the world, Woods et al. (2016), were able to evaluate the impact of global phenomenon, such as the El-Nino-Southern oscillation (ENSO) on the increase in DNB incidence and severity. They found that since the 1950s, four of the past five strong ENSO events, which influence patterns of temperature and precipitation in many regions of the world often resulting in warmer and wetter conditions have coincided with reports of increase DNB activity on an intercontinental scale.

Given the above information, future climatic conditions predicted for several forested regions in the Northern Hemisphere appear to be increasingly favorable for both DNB and WPND. The global increase in incidence and severity of *L. acicola* over the last decade is very similar to the rise of DNB 50 years ago. While *L. acicola* is native to Central and South America, an increase in incidence and severity has been reported from the northeastern U.S. (Broders et al., 2015; Wyka et al., 2017a), as well as in Europe including reports from Austria (Hintsteiner et al., 2012), Czech Republic (Jankovsky et al., 2009), Estonia (Adamson et al., 2015), Italy (La Porta and Capretti, 2000), Lithuania (Markovskaja et al., 2011), Slovenia (Jurc and Jurc, 2010), Spain (Ortiz de Urbina et al., 2017) and Switzerland (Holdenrieder and Sieber, 1995). The arrival of *L. acicola* in Europe is relatively recent and it is still unclear what the long-term impact of this pathogen will have on the region, but it could be expected that impacts on individual tree health will result in reduced growth (Welsh et al., 2009). A recent study from Spain has indicated that all three fungal pathogens (*D. pini*, *D. septosporum* and *L. acicola*) are widely distributed in exotic and native pine plantations and have caused severe defoliation and mortality in regions where the pathogens had not previously been detected (Ortiz de Urbina et al., 2017). Disease incidence and severity of *L. acicola* has also continued to increase in more northern European counties such as Estonia, which has seen an increase in the distribution and host range of the disease since it was first reported in 2008 (Adamson et al., 2015). We need to learn the lessons of DNB and develop a global network in order to monitor the incidence and severity of *L. acicola* as well as develop disease risk maps based on current epidemiological data in order to predict where brown spot needle blight will become more severe in the future. This will assist both researchers and policy makers in developing disease mitigation and control strategies.

##### 4.2. Similarities between Swiss needle cast in Oregon and white pine needle damage

Similar to WPND and DNB, Swiss Needle Cast (SNC) is caused by a native pathogen, *Phaeocryptopus gaeumannii* (Rodhe) Petr. that was present in Oregon Douglas-fir (*Pseudotsuga menziesii* (Mirb.) stands for decades, but did not reach epidemic levels until 1990s (Manter et al., 2005; Shaw et al., 2011). Data from long-term monitoring plots show that SNC epidemic has continued to intensify since the 1990s (Ritkova et al., 2016). Disease expression is related to provenance and local

climate as demonstrated by seed-source movement trials in Oregon (Wilhelmi et al., 2017). Widespread disease distribution across multiple-ownerships, stand ages, and management histories, however, suggests that planting of inappropriate seed source is unlikely to be the primary cause of the epidemic (Manter et al., 2005). An increase in the amount of coastal lands converted to Douglas-fir plantations coupled with climatic conditions more favorable to the growth and reproduction of the fungus likely contributed to the increase of SNC above historic levels (Manter et al., 2005). The abundance of SNC inoculum in Oregon is positively correlated with winter mean daily temperature and needle wetness hours during spring (Manter et al., 2005). Similar to WPND, foliar symptoms of SNC such as needle retention is also affected by winter temperature and spring and summer precipitation among other variables (Zhao et al., 2011; Wyka et al., 2017a). Long term climate predictions for Oregon indicate that conditions favorable for the reproduction and dispersal of the pathogen, and thus development of SNC epidemics, such as winter temperature and spring precipitation will continue to increase (Manter et al., 2005; Lee et al., 2013) at least in some geographic locations (Agne et al., 2018). In addition, increased temperatures and wetness during reproductive season of the SNC pathogen lead to greater disease severity parallels predictions for WPND (Wyka et al., 2017a) and DNB (Woods et al., 2016). Also similar, are the effects of these pathogens on host physiology as all have been shown to reduce growth of their host (Welsh et al., 2009; Lee et al., 2013; Lee et al., 2017).

#### 4.3. Stressed trees and *Diplodia* shoot blight and canker

*Diplodia* shoot blight and canker, caused by *Diplodia sapinea* (Fr.) Fuckel and *D. scrobiculata* J. de Wet, Slippers & M.J. Wingf., cause damage to conifers in plantations and natural settings throughout the world (Swart and Wingfield, 1991; Fabre et al., 2011). Canker pathogens such as *Diplodia* are often associated with conditions that induce host stress such as drought, hail storms or winter damage (Swart and Wingfield, 1991; Desprez-Loustau et al., 2007; Fabre et al., 2011; Chhin and O'Brien, 2015). Projected increases in temperature and precipitation projected from atmosphere-ocean general circulation models should favor the growth and reproduction of the pathogen directly (Peterson, 1977; Fabre et al., 2011). *Diplodia* shoot blight and canker disease severity is likely to also be affected indirectly by changing host physiology. Drought stress, for example, is associated with increased *Diplodia* canker disease severity (Blodgett et al., 1997; Desprez-Loustau et al., 2006). Other stresses such as wounding from hail or winter storms are also associated with *Diplodia* canker outbreaks (Swart and Wingfield, 1991; Chhin and O'Brien, 2015). White pine is a host for the more aggressive *D. sapinea*, but red pine (*Pinus resinosa* Aiton) is more susceptible. Consequently, in Northeastern USA, *Diplodia* shoot blight and canker is common in red pine plantations and natural stands (Ostry et al., 2012).

#### 4.4. Stressed trees and *Caliciopsis* canker

Analogous to the foliar and canker diseases described above, *Caliciopsis* canker is caused by a native pathogen, *Caliciopsis pinea*, and it has also become an emerging disease in the past two of decades (Lombard and Bofinger, 1999; Asaro, 2011; Munck et al., 2015a). Unlike *Diplodia* canker, the epidemiology of *Caliciopsis* canker is poorly understood. *Caliciopsis* canker is associated with the eastern white pine scale, *Matsucoccus macrocaticricies* Richards (Hemiptera: Matsucoccidae), a piercing and sucking insect pest (Mech et al., 2013; Asaro et al., 2017; Shultz et al., 2018, this issue). Warmer winters are likely to improve survival of both the scale insect and the pathogen, *C. pinea*. The pathogen is dispersed by splashing rainwater and thus wetter growing seasons would be expected to favor its reproduction and dispersal. Similar to *Diplodia* canker, disease incidence and severity is associated with factors leading to poor host condition such as high

density stands and nutrient poor, excessive drained soils (Munck et al., 2016). *Diplodia* canker severity in red pine plantations in Wisconsin was also greater in excessively drained soils (Munck et al., 2009). Drier soils are more conducive to drought stress which predisposes trees to canker pathogens. While mortality from these canker pathogens alone are fairly uncommon, *Diplodia* and *Caliciopsis* canker pose a threat to the eastern white pine lumber industry as infections reduce growth rates and highly degrade the value of the wood product (Costanza et al., 2018 *In review*).

#### 4.5. White pine blister rust predictions for the northeast

Unlike the foliar and canker pathogens previously described, WPBR is caused by an exotic pathogen, *Cronartium ribicola* (J.C. Fisch.). Although lack of host resistance is likely to play a larger role in the epidemiology of this disease than changes in the environment, increased precipitation is expected to favor its sporulation and spore dispersal (Dukes et al., 2009). WPBR disease incidence has persisted at low levels in the northeast for many decades after high rates of white pine mortality and intensive management efforts from the early to middle 20th century (Lombard and Bofinger, 1999; Geils et al., 2010). *Ribes* eradication efforts and a dominance of mature white pines, which are less susceptible to the disease than regeneration, are two of several possible explanations for the low levels of disease incidence (Lombard and Bofinger, 1999). Since the discovery of a strain of *C. ribicola* that had overcome the immunity bred into a widely planted cultivar of black currant (*Ribes nigrum* cv. Titania) in Connecticut, there has been renewed interest in the disease (Frederick et al., 2011). A survey of plantations composed of immune *Ribes* cultivars and surrounding forests of eastern white pine found a correlation between incidence of WPBR on previously immune *Ribes* and adjacent white pines (Munck et al., 2015b). Detailed studies related to disease incidence and climate have not been conducted recently. Given the changing climate, the economic importance of white pine in the region, the cultivation of *Ribes* cultivars no longer resistant to blister rust, and historic high mortality rates caused by WPBR, it would be important to investigate how our current climatic conditions might be affecting disease development.

### 5. Impact of climate change on the *Pinus strobus* ecosystem

Based on future climate change projections, Joyce and Rehfeldt (2013) modeled the future range distribution of *P. strobus* and observed a clear northward shift in suitable habitat for the species. The greatest impact will be early and sustained deterioration in the species' contemporary habitat, especially in southern states (Joyce and Rehfeldt, 2013). Concurrence among climate change projections to the north of the contemporary distribution identified geographic locations with the highest probability of supporting vigorous stands of *P. strobus*. While new potential stands were identified, the overall distribution of *P. strobus* is expected to shrink as geographic limits to the north will prevent further movement of the species (Joyce and Rehfeldt, 2013).

So what will be the long-term effects of pathogens and climate change on *P. strobus* and the ecosystems dominated by this species? Trees store nonstructural carbohydrates (NSC; i.e. sugars and starch) as reserves to support metabolic functions and growth, particularly following abiotic or biotic stress (Dietze et al., 2014). Recent studies show that sustained defoliation events, triggered by drought or fungal pathogens, significantly impact the allocation of NSCs and thus compromise tree growth, photosynthesis, and stress response (Dietze et al., 2014; McDowell et al., 2008; Saffell et al., 2014). Doug-fir infected by SNC, exhibits a shift in NSC allocation to the crown at the expense of trunk radial growth (Saffell et al., 2014). Changes in NSC allocation in white pine in response to repeated WPND infestation could have similar impacts on the health, growth, and survival of this species. WPND-induced disruption of NSC allocation to radial growth would greatly

reduce productivity of white pine as a timber product.

Ecosystem theory suggests that pathogen outbreaks that alter host or community characteristics will, in turn, alter ecosystem processes such as C and N cycling, litterfall dynamics, and decomposition (Ellison et al., 2005; Lovett et al., 2006). However, few field studies have quantified how interactions between pathogens and global change drivers influence ecosystem scale patterns and processes (Hicke et al., 2012). For example, foliar chemistry changes caused by foliar-feeding insects have been linked to altered litterfall chemistry and decomposition rates (Chapman et al., 2006; Lovett et al., 2006; Russell et al., 2004). Recent studies have demonstrated that significant defoliations and loss of foliar biomass are caused by WPND (Wyka et al., 2017b; McIntire et al., *In Review*) and the negative impact of these repeated defoliation events on tree productivity (McIntire et al., 2014), may alter ecosystem C and N cycles. For instance, summer defoliation due to insect herbivory in hardwood species resulted in a redistribution of N, disrupting the natural processes of N resorption from leaves in the autumn and reducing trees' internal cache of N (Lovett et al., 2002). Needles dropped in June and July induced by WPND contains higher concentrations of N compared to the natural litter fall in autumn, where the fate of N will accumulate in soil rather than resorbed within the tree (McIntire et al., *In Review*). It has been suggested that in cases where defoliation is chronic and severe enough to cause widespread mortality, increased N loss could result through leaching due to soil retention of N becoming inundated (Lovett et al., 2002). Variability in climate may exacerbate the problem if wetter and warmer-than-average springs and summer droughts persist in the future.

## 6. Management of forest lands

Land managers will have to take into account uncertainty in relation to climate change effects on tree hosts and associated pathogens (Dukes et al., 2009). Maintaining adequate stand density will be necessary to reduce stress caused by changing climatic condition and damage from pathogens (Leak and Lamson, 1999). For example, thinning increases climatic resilience of red pine (Magruder et al., 2013). Thinning has also been initially successful at ameliorating foliar symptoms of WPND (McIntire et al., 2018 *this issue*). Reducing competition will help residual trees to withstand adverse conditions by increasing their access to sunlight and space. Maintaining adequate stocking in white pine stands growing on excessively drained, nutrient poor sites will likely reduce damage from *Caliciopsis* canker and foliar diseases (Leak and Lamson, 1999; Munck et al., 2016). Reducing stand density should also reduce relative humidity and leaf wetness duration within the canopy of white pines which could reduce conditions conducive for spore production and dispersal of the foliar pathogens associated with WPND.

## 7. Conclusions

Forecasting the effects of climate change on individual pathogens is a challenging task, especially in natural forest settings with long-lived hosts and short generation times of pathogens (Brasier, 2001; Sturrock et al., 2011). This task further complicated when the actions of foliar pathogens (WPND) can weaken trees and affect the subsequent infection of eastern white pine by white pine blister rust, root and butt rot fungi (*Armillaria ostoyae* and *A. mellea*), and canker pathogens (*Caliciopsis pinea* and *Diplodia sapinea*); with all three pathogen types showing varied responses to different climatic and environmental factors (Dukes et al., 2009; Brazee and Wick, 2011; Munck et al., 2015a,b, 2016; Wyka et al., 2017a,b). Despite showing varied responses, it appears that the climate and environmental shifts occurring in north-eastern North America are favoring all three of these eastern white pine diseases groups.

Climate change forecasts predict a wetter and warmer climate for the region with temperatures expected to increase for all months while precipitation is expected to increase in every season except summer

(Hayhoe et al., 2007; Campbell et al., 2011). These increases should theoretically be positive for plant growth as Luo (2007) and Anderson et al. (2006) determined that trees will have a higher metabolic process which leads to higher biomass accumulation as temperatures rise with coinciding adequate precipitation. However, early defoliation of eastern white pine caused by WPND has been shown to significantly reduce needle biomass throughout the growing season which implies a decreases photosynthetic capacity and overall negative affect on tree development. Due to the long-lived nature of trees and the relatively short generation time of pathogens, it appears that these wetter and warmer springs will favor the reproduction and dispersal of the foliar WPND, over the positive effects on tree development, resulting in repeated defoliations and chronically stressed trees. Such stressed trees are subsequently under increased threat of infection by *Armillaria* species which are expected to have extended growing seasons due to increases in temperature. Furthermore, the predicted decrease in summer precipitation (Campbell et al., 2011) coupled with increases in temperature could result in water deficits leading to drought stress in eastern white pines which predisposes trees to infection by *Caliciopsis* and *Diplodia* canker (Blodgett et al., 1997; Desprez-Loustau et al., 2006; Munck et al., 2009, 2015). Further research into the interactions between foliar pathogens, root, butt and trunk rot fungi, and stem and branch canker fungi is needed to determine if the recent decline in eastern white pine will continue. The outlook for eastern white pine is not particularly bright, but certainly taking a proactive approach will help to reduce potential ecosystem loss. For instance, white pine density management can help to mitigate the effects of these damaging agents (McIntire et al., 2018 *this issue*).

Knowledge from similar forest pathogen systems, particularly DNB (Woods et al., 2016) and SNC (Manter et al., 2005) can provide a good proxy to estimate the potential increases in global expansion and disease severity for WPND throughout northeastern North America and Europe. Utilizing new tools such as host layer mapping (Wyka et al., 2017a) and GIS layers of soils, hardness zones, slopes and aspects (Munck et al., 2015) can help in evaluating high-risk zones and aid ground based sampling efforts to better predict the distribution and future spread of eastern white pine pathogens. Combining this knowledge with current epidemiological data and accurate climatic data will facilitate the development of disease risk maps which will assist researchers and policy makers in developing disease mitigation and control strategies.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.03.011>.

## References

- Abrams, M.D., 2001. Eastern white pine versatility in the presettlement forest. *Bioscience* 51, 967–979.
- Adamson, K., Drenkhan, R., Hanso, M., 2015. Invasive brown spot needle blight caused by *Lecanosticta acicola* in Estonia. *Scand. J. For. Res.* 30, 587–593.
- Agne, M.C., Beedlow, P.A., Shaw, D.C., Woodruff, D.R., Lee, E.H., Cline, S.P., Comeleo, R.L., 2018. Interactions of predominant insects and diseases with climate change in Douglas-fir forests of western Oregon and Washington, U.S.A. *For. Ecol. Manage.* 409, 317–332.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
- Anderson, K.J., Allen, A.P., Gillooly, J.F., Brown, J.H., 2006. Temperature-dependence of biomass accumulation rates during secondary succession. *Ecol. Lett.* 9, 673–682.



- Asaro, C., 2011. What is killing white pine in the highlands of West Virginia? In: Forest Health Review May 2011. Virginia Department of Forestry, Charlottesville, VA.
- Asaro, C., Chamberlin, L.A., Rose, J.A., Mooneyham, K., Rose, A.K., 2017. Mortality of eastern white pine (*Pinus strobus* L.) in association with a novel scale insect-pathogen complex in Virginia and West Virginia. *For. Ecol. Manage.*
- Barnes, I., Crous, P.W., Wingfield, B.D., Wingfield, M.J., 2004. Multigene phylogenies reveal that red band needle blight of *Pinus* is caused by two distinct species of *Dothistroma*, *D. septosporum* and *D. pini*. *Stud. Mycol.* 50, 551–565.
- Basham, J.T., Morawski, Z.J.R., 1964. Cull studies, the defects and associated basidiomycete fungi in the heartwood of living trees in the forests of Ontario. Canadian Department of Forestry Publication No. 1072.
- Benedict, W.V. 1981. History of white pine blister rust control—a personal account. Rep. FS-355. Washington, DC: U.S. Department of Agriculture, Forest Service, 47 p.
- Benoit, L.F., Skelly, J.M., Moore, L.D., Dochinger, L.S., 1982. Radial growth reductions of *Pinus strobus* L correlated with foliar ozone sensitivity as an indicator of ozone-induced losses in eastern forests. *Can. J. For. Res.-Revue Canad. De Recherche Forestiere* 12, 673–678.
- Betts, H.S., 1954. Eastern white pine (*Pinus strobus*). USDA Forest Service. Available: < <http://www.fpl.fs.fed.us/documnts/usda/amwood/ewhpine.pdf> > .
- Blodgett, J.T., Kruger, E.L., Stanosz, G.R., 1997. *Sphaeropsis sapinea* and Water Stress in a Red Pine Plantation in Central Wisconsin. *Phytopathology* 87, 429–434.
- Boyce Jr., J.S., 1959. Brown spot needle blight on eastern white pine. *Plant Disease Reporter* 43, 420.
- Bradshaw, R.E., 2004. Dothistroma (red-band) needle blight of pines and the dothistromin toxin: a review. *Forest Pathol.* 34, 163–185.
- Brasier, C.M., 2001. Rapid evolution of introduced plant pathogens via interspecific Hybridization. *Bioscience* 51, 123–133.
- Braze, N.J., Wick, R.L., 2011. *Armillaria* species distribution and site relationships in *Pinus*- and *Tsuga*-dominated forests in Massachusetts. *Can. J. For. Res.-Revue Canadienne De Recherche Forestiere* 41, 1477–1490.
- Broders, K., Munck, L., Wyka, S., Iriarte, G., Beaudoin, E., 2015. Characterization of fungal pathogens associated with white pine needle damage (WPND) in Northeastern North America. *Forests* 6, 4088–4104.
- Bulman, L.S., Dick, M.A., Ganley, R.J., McDougal, R.L., Schwelm, A., Bradshaw, R.E., 2013. Dothistroma Needle Blight. *Infect. For. Dis.* 436–457.
- Burdon, J.J., Thrall, P.H., Nemri, A., 2012. Approaches to understanding the impact of life-history features on plant-pathogen co-evolutionary dynamics. In: Snieszko, R., Yanchuk A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel, S.J. (Eds.), *Proceedings of the Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees*, pp. 104–111, Gen. Tech. Rep. PSW-GTR-240. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.
- Campbell, J.L., Driscoll, C.T., Pourmokhtarian, A., Hayhoe, K., 2011. Streamflow responses to past and projected future changes in climate at the Hubbard Brook Experimental Forest, New Hampshire, United States. *Water Resources Res.* 47.
- Campbell, J.L., Ollinger, S.V., Flerchinger, G.N., Wicklein, H., Hayhoe, K., Bailey, A.S., 2010. Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Hydrol. Process* 2, 2465–2480.
- Chandelier, P., Lafaurie, C., Maugard, F., 1994. The discovery in France of *Mycosphaerella dearnessii*, on *Pinus attenuata* X *radiata*. *Comptes Rendus de l'Academie d'Agriculture de France* 80, 103–108.
- Chapman, S.K., Schweitzer, J.A., Whitham, T.G., 2006. Herbivory differentially alters plant litter dynamics of evergreen and deciduous trees. *Oikos* 114, 566–574.
- Charlton, J.W., 1963. Relating climate to eastern white pine blister rust infection hazard. *USDA For. Serv. Northeast. For. Exp. Stn.* 38 p.
- Chhin, S., O'Brien, J., 2015. Dendroclimatic analysis of red pine affected by Diplodia shoot blight in different latitudinal regions in Michigan. *Can. J. For. Res.* 45, 1757–1767.
- Costanza K.K.L., T.D. Whitney, W.H. Livingston, C.D. McIntire, K.J.K. Gandhi., In review. Health, ecology, and management of eastern white pine (*Pinus strobus* L.) across eastern North America. *Forest Ecol. Manage.*
- de Urbina, E.O., Mesanza, N., Aragones, A., Raposo, R., Elvira-Recuenco, M., Boque, R., Patten, C., Aitken, J., Iturriza, E., 2017. Emerging Needle Blight Diseases in Atlantic Pinus Ecosystems of Spain. *Forests* 8.
- Desprez-Loustau, M.L., Robin, C., Reynaud, G., Deque, M., Badeau, V., Piou, D., Husson, C., Marçais, B., 2007. Simulating the effects of a climate-change scenario on the geographical range and activity of forest-pathogenic fungi. *Can. J. Plant Pathol.-Revue Canadienne De Phytopathologie* 29, 101–120.
- Desprez-Loustau, M.L., Benoit, M., Louis-Michel, N., Dominique, P., Andrea, V., 2006. Interactive effects of drought and pathogens in forest trees. *Ann. For. Sci.* 63, 597–612.
- Dietze, M.C., Sala, A., Carbone, M.S., Czimczik, C.I., Mantooth, J.A., Richardson, A.D., Vargas, R., 2014. Nonstructural carbon in woody plants. *Ann. Rev. Plant Biol.* 65, 667–687.
- Drenkhan, R., Adamson, K., Jurimaa, K., Hanso, M., 2014. *Dothistroma septosporum* on firs (*Abies spp.*) in the northern Baltics. *Forest Pathol.* 44, 250–254.
- Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Braze, N., Cooke, B., Theoharides, K.A., Stange, E.E., Harrington, R., Ehrenfeld, J., Gurevitch, J., Lerdau, M., Stinson, K., Wick, R., Ayres, M., 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Can. J. Forest Res.-Revue Canadienne De Recherche Forestiere* 39, 231–248.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3, 479–486.
- Fabre, B., Piou, D., Desprez-Loustau, M.L., Marçais, B., 2011. Can the emergence of pine Diplodia shoot blight in France be explained by changes in pathogen pressure linked to climate change? *Glob. Change Biol.* 17, 3218–3227.
- Foster, D.R., 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *J. Ecol.* 80, 753–771.
- Frant, B., Lilja, R., Weeks, M., 2011. 2010 Aerial Detection Survey Results: Durham Field Office, Forest Health Management, USDA Forest Service. < [https://www.fs.fed.us/foresthealth/docs/fhh/ME\\_FHH\\_2010.pdf](https://www.fs.fed.us/foresthealth/docs/fhh/ME_FHH_2010.pdf) > .
- Frederick, Z.A., Villani, S., Cox, K.D., 2011. First report of white pine blister rust caused by *Cronartium ribicola* on immune black currant *Ribes nigrum* Cv. Titania in Preston, Connecticut. *Plant Dis.* 95, 1589.
- Frumhoff, P.C., McCarthy, J.J., Melillo, J.M., Moser, S.C., Wuebbles, D.J., 2007. Confronting Climate Change in the U.S. Northeast. Synthesis report of the Northeast Climate Impact Assessment (NECIA). Cambridge, MA: Union of Concerned Scientist (UCS).
- Garrett, K.A., Dendy, S.P., Frank, E.E., Rouse, M.N., Travers, S.E., 2006. Climate change effects on plant disease: genomes to ecosystems. *Ann. Rev. Phytopathol.* 44, 489–509.
- Geils, B.W., Hummer, K.E., Hunt, R.S., 2010. White pines, *Ribes*, and blister rust: a review and synthesis. *Forest Pathol.* 40, 147–185.
- Gibson, I.A.S., 1972. Dothistroma blight on *Pinus radiata*. *Ann. Rev. Phytopathol.* 10 51–8.
- Gray, L.K., Russel, J.H., Yanchuk, A.D., Hawkins, B.J., 2013. Predicting the risk of cedar leaf blight (*Didymascella thujina*) in British Columbia under future climate change. *Agric. Forest Meteorol.* 180, 152–163.
- Hansen, E.M., Lewis, K.J., 1997. *Compendium Conifer Diseases*. APS Press, St. Paul, MN, USA.
- Harrison, K.J., 2009. Forest disease records on eastern white pine in Atlantic Canada: 1950 to 1996. *For. Chron.* 85, 604–608.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfield, R.S., Samuel, M.D., 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296, 2158–2162.
- Hayhoe, K., Wake, C.P., Huntington, T.G., Luo, L., Schwartz, M.D., Sheffield, J., Wood, E., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T.J., Wolfe, D., 2007. Past and future changes in climate and hydrological indicators in the US Northeast. *Clim. Dyn.* 28, 381–407.
- Heimann, M.F., Stanosz, G.R., and Worf, G.L. 1997. Pine needle diseases: Brown spot and Lophodermium needlecast. University of Wisconsin-Extension. Available: <http://learningstore.uwex.edu/assets/pdfs/A2608.pdf>.
- Hepting, G.H., 1971. *Diseases of Forest and Shade Trees of the United States*. Washington, DC: USDA Agricultural Handbook No. 36.
- Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Hogg, E.H., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N., Vogelmann, J., 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Glob. Change Biol.* 18, 7–34.
- Hintsteiner, M., Cech, T.L., Halmshlager, E., Stauffer, C., Kirisits, T., 2012. First report of *Mycosphaerella dearnessii* on *Pinus nigra* var. *nigra* in Austria. *Forest Pathol.* 42, 437–440.
- Holdenrieder, O., Sieber, T.N., 1995. First report of *Mycosphaerella dearnessii* in Switzerland. *Eur. J. For. Pathol.* 25, 293–295.
- Huang, Z.Y., Smalley, E.B., Guries, R.P., 1995. Differentiation of *Mycosphaerella dearnessii* by cultural characters and RAPD analysis. *Phytopathology* 85, 522–527.
- Jankovsky, L., Palovcikov, D., Tomsovsky, M., 2009. Brown spot needle blight associated with *Mycosphaerella dearnessii* occurs on *Pinus rotundata* in the Czech Republic. *Plant. Pathol.* 58 398–398.
- Joyce, D.G., Rehfeldt, G.E., 2013. Climatic niche, ecological genetics, and impact of climate change on eastern white pine (*Pinus strobus* L.): Guidelines for land managers. *For. Ecol. Manage.* 295, 173–192.
- Jurc, D., Jurc, M., 2010. *Mycosphaerella dearnessii* occurs in Slovenia. *Plant. Pathol.* 59 808–808.
- La Porta, N., Capretti, P., 2000. *Mycosphaerella dearnessii*, a Needle-cast Pathogen on Mountain Pine (*Pinus mugo*) in Italy. *Plant Dis.* 84 922–922.
- Leak, W.B., Lamson, N.I., 1999. Revised white pine stocking guide for managed stands. In: U.S. Department of Agriculture, F.S., Northeastern Area State and Private Forestry (Ed.), *USDA, Forest Service*, p. 2.
- Lee, E.H., Beedlow, P.A., Waschmann, R.S., Burdick, C.A., Shaw, D.C., 2013. Tree-ring analysis of the fungal disease Swiss needle cast in western Oregon coastal forests. *Can. J. For. Res.* 43, 677–690.
- Lee, E.H., Beedlow, P.A., Waschmann, R.S., Tingey, D.T., Cline, S., Bollman, M., Wickham, C., Carlile, C., 2017. Regional patterns of increasing Swiss needle cast impacts on Douglas-fir growth with warming temperatures. *Ecol. Evol.* 7, 11167–11196.
- Lombard, K., Bofinger, J., 1999. White pine blister rust, *Cronartium ribicola*, infestation incidence for selected areas of New Hampshire. In: New Hampshire Department of Resources and Economic Development, Division of Forests and Lands, Durham, NH, p. 11.
- Luo, Y., 2007. Terrestrial carbon-cycle feedback to climate warming. *Annu. Rev. Ecol. Syst.* 38, 683–712.
- Lovett, G.M., Christenson, L.M., Groffman, P.M., Jones, C.G., Hart, J.E., Mitchell, M.J., 2002. Insect defoliation and nitrogen cycling in forests: laboratory, plot, and watershed studies indicate that most of the nitrogen releases from forest foliage as a result of defoliation by insects is redistributed within the ecosystem, whereas only a small fraction of nitrogen is lost by leaching. *Bioscience* 52, 335–341.
- Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* 56, 395–405.
- Magruder, M., Chhin, S., Palik, B., Bradford, J.B., 2013. Thinning increases climatic



- resilience of red pine. *Can. J. For. Res.* 43, 878–889.
- Maguire, D.A., Kanaskie, A., Voelker, W., Johnson, R., Johnson, G., 2002. Growth of young Douglas-fir plantations across a gradient in Swiss needle cast severity. *West. J. Appl. For.* 17, 86–95.
- Manion, P.D., 1981. *Tree Disease Concepts*. Prentice-Hall Inc., Englewood Cliffs, New Jersey.
- Manter, D.K., Reeser, P.W., Stone, J.K., 2005. A climate-based model for predicting geographic variation in Swiss needle cast severity in the Oregon Coast Range. *Phytopathology* 95, 1256–1265.
- Marchetti, S.B., Worrall, J.J., Eager, T., 2011. Secondary insects and diseases contribute to sudden aspen decline in southwestern Colorado, USA. *Can. J. For. Res.* 41, 2315–2325.
- Markovskaja, S., Kacergius, A., Treigienė, A., 2011. Occurrence of new alien pathogenic fungus *Mycosphaerella deaneessii* in Lithuania. *Botanica Lithuanica* 17, 29–37.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.* 26, 523–532.
- McIntire, C.D., Munck, I., Vadeboncoeur, M.A., Livingston, W., Asbjornsen, H. In Review. Impacts of White Pine Needle Damage on seasonal litterfall dynamics and wood growth of eastern white pine (*Pinus strobus*) in New England. *FEM*.
- McIntire et al., 2018. Thinning treatments reduce severity of foliar pathogens in eastern white pine. *FEM*: this issue.
- McIntire, C., Asbjornsen, H., Broders, K., Munck, I., Livingston, W., 2014. Interactive effects of white pine needle damage and climate change on forest health and carbon-water dynamics across the northeastern United States. *The International Forestry Review* 16: 486. Presentation at XXIV IUFRO World Congress.
- McLaughlin, S.B., McConathy, R.K., Duvick, D., Mann, L.K., 1982. Effects of chronic air-pollution stress on photosynthesis, carbon allocation, and growth of white-pine trees. *Forest Sci.* 28, 60–70.
- Mech, A.M., Asaro, C., Cram, M.M., Coyle, D.R., Gullan, P.J., Cook, L.G., Gandhi, K.J.K., 2013. *Matsucoccus macrocicatricis* (Hemiptera: Matsucoccidae): First report, distribution, and association with symptomatic eastern white pine in the Southeastern United States. *J. Econ. Entomol.* 106, 2391–2398.
- Merrill, W., Wenner, N.G., Dreisbach, T.A., 1996. *Canavirgella banfieldii* gen and sp nov: A needlecast fungus on pine. *Can. J. Botany-Revue Canadienne De Botanique* 74, 1476–1481.
- Mielke, J.L., 1943. White pine blister rust in western North America. *School of Forestry Bull.* 52, Yale Univ., New Haven, CT, 155 p.
- Minter, D.W., Millar, C.S., 1984. *Bifusella linearis*. IMI Descriptions of Fungi and Bacteria. CABI Bioscience, Bakeham Lane, Egham, Surrey, TW20 9TY, UK. (Abstr.)
- Morrison, D.J., 2004. Rhizomorph growth habit, saprophytic ability and virulence of 15 *Armillaria* species. *Forest Pathol.* 34, 15–26.
- Munck, A.I., Luther, T., Wyka, S., Keirstead, D., McCracken, K., Ostrofsky, W., Searles, W., Lombard, K., Weimer, J., Allen, B., 2016. Soil and Stocking Effects on Caliciopsis Canker of *Pinus strobus* L. *Forests* 7.
- Munck, I.A., Livingston, W., Lombard, K., Luther, T., Ostrofsky, W.D., Weimer, J., Wyka, S., Broders, K., 2015a. Extent and severity of Caliciopsis canker in New England, USA: An emerging disease of eastern white pine (*Pinus strobus* L.). *Forests* 6, 4360–4373.
- Munck, A.I., Tanguay, P., Weimer, J., Villani, S.M., Cox, K.D., 2015b. Impact of white pine blister rust on resistant cultivated Ribes and neighboring eastern white pine in New Hampshire. *Plant Disease* 99, 1374–1382.
- Munck, I.A., Ostrofsky, W.D., Burns, B., 2011. Eastern White Pine Needle Damage. In: USDA Forest Service, Northeastern Area, State & Private Forestry, 11 Campus Boulevard, Suite 200 Newtown Square, PA 19073.
- Munck, I.A., Smith, D.R., Sickley, T., Stanosz, G.R., 2009. Site-related influences on cone-borne inoculum and asymptomatic persistence of *Diplodia* shoot blight fungi on or in mature red pines. *For. Ecol. Manage.* 257, 812–819.
- NRCC/Northeast Regional Climatic Center. 2017. Monthly Maps. Available: <http://www.nrcc.cornell.edu/regional/monthly/monthly.html>.
- NOAA/National Climatic Data Center, 2015. Land-based station data. Available: <http://www.ncdc.noaa.gov/data-access/land-based-station-data>.
- Ostrofsky, W.D., Rumpf, T., Struble, D., Bradbury, R., 1988. Incidence of white pine blister rust in Maine after 70 years of Ribes eradication program. *Plant Dis.* 72, 967–970.
- Ostry, M.E., Moore, M.J., Kern, C.C., Venette, R.C., Palik, B.J., 2012. Multiple diseases impact survival of pine species planted in red pine stands harvested in spatially variable retention patterns. *For. Ecol. Manage.* 286, 66–72.
- Peterson, G.W., 1977. Infection, epidemiology, and control of *Diplodia* blight of austrian, ponderosa, and scots pines. *Phytopathology* 67, 511–514.
- Phelps, W.R., Kais, A.G., Nicholls, T.H. 1978. Brown-spot needle blight of pines. USDA, Forest Insect and Disease Leaflet 44.
- Ritokova, G., Shaw, D.C., Filip, G., Kanaskie, A., Browning, J., Norlander, D., 2016. Swiss needle cast in Western Oregon Douglas-Fir Plantations: 20-Year monitoring results. *Forests* 7.
- Rock, B.N., Carlson, M., 2013. Forest Watch Data Book 2012-2013: Research with 2011 Needles. Forest Watch, University of New Hampshire, Durham, NH. Available: <http://www.forestwatch.sr.unh.edu/data/data.shtml>.
- Russell, C.A., Kosola, K.R., Paul, E.A., Robertson, G.P., 2004. Nitrogen cycling in poplar stands defoliated by insects. *Biogeochemistry* 68, 365–381.
- Saffell, B.J., Meinzer, F.C., Woodruff, D.R., Shaw, D.C., Voelker, S.L., Lachenbruch, B., Falk, K., 2014. Seasonal carbohydrate dynamics and growth in Douglas-fir trees experiencing chronic, fungal-mediated reduction in functional leaf area. *Tree Physiol.* 34, 218–228.
- Shaw, C.G., Toes, E.H.A., 1977. Impact of dothistroma needle blight and armillaria root-rot on diameter growth of *Pinus radiata*. *Phytopathology* 67, 1319–1323.
- Shaw, D.C., Filip, G.M., Kanaskie, A., Maguire, D.A., Littke, W.A., 2011. Managing an epidemic of swiss needle cast in the Douglas-Fir region of Oregon: the role of the swiss needle cast cooperative. *J. Forestry* 109, 109–119.
- Shultz et al. 2018. Assessment of abiotic and biotic factors associated with Eastern White Pine (*Pinus strobus* L.) dieback in the Southern Appalachian Mountains. *Forest Ecol. Manage.*: this issue.
- Siggers, P.V. 1944. The brown spot needle blight of pine seedlings. U.S. Dep. Agric., Technical Bulletin 870:1-36.
- Silverberg, S.B., Gilbertson, R.L., 1962. *Tree Diseases in New York State Plantations: A Field Manual*. Bulletin No. 44, State University College of Forestry, Syracuse, New York.
- Sinclair, W.A., Lyon, H.H., 2005. *Diseases of Trees and Shrubs*, second ed. Comstock Pub. Associates/Cornell University Press, Ithaca, New York.
- Skilling, D.D., Nicholls, T.H. 1974. Brown spot needle disease – biology and control in Scots pine plantations. USDA For. Serv., Research Paper NC-109.
- Spaulding, P., 1952. Root rots of conifers. In: Baldwin, H.I., Brown, R.C., Hansbrough, J.R., Peirson, H.B., Reed, P.M., Reynolds, H.A., Rathburn, L.W. (Eds.), *Important Tree Pests of the Northeast*. Society of American Foresters, Concord, New Hampshire, pp. 138–141.
- Stanosz, G., Cummings, J., Jackson, W., 1991. Pest Alert: Brown spot needle blight of eastern white pine. USDA Forest Service, Northeastern Area, NA-PR-03-91.
- Smith, J.P., Hoffman, J.T., 2000. Status of white pine blister rust in the Intermountain West. *Western North Am. Naturalist* 60, 165–179.
- Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J., Woods, A.J., 2011. Climate change and forest diseases. *Plant. Pathol.* 60, 133–149.
- Swart, W.J., Wingfield, M.J., 1991. Biology and control of *Sphaeropsis sapinea* on *Pinus* species in south-africa. *Plant Dis.* 75, 761–766.
- Thompson, J.R., Carpenter, D.N., Cogbill, C.V., Foster, D.R., 2013. Four centuries of change in Northeastern United States forests. *Plos One* 8.
- Vadeboncoeur, M.A., Hamburg, S.P., Cogbill, C.V., Sugimura, W.Y., 2012. A comparison of presettlement and modern forest composition along an elevation gradient in central New Hampshire. *Can. J. For. Res.* 42, 190–202.
- Videira, S.I.R., Groenewald, J.Z., Nakashima, C., Braun, U., Barretto, R.W., de Wit, P.J.G.M., Crous, P.W., 2017. *Mycosphaerellaceae* – Chaos of clarity? *Stud. Mycol.* <http://dx.doi.org/10.1016/j.simyco.2017.09.003>.
- Welsh, C., Lewis, K., Woods, A., 2009. The outbreak history of Dothistroma needle blight: an emerging forest disease in northwestern British Columbia, Canada. *Can. J. For. Res.-Revue Canadienne De Recherche Forestiere* 39, 2505–2519.
- Wendel, G.W., Smith, H.C., 1990. Eastern White Pine (*Pinus strobus* L.). In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America, Agriculture Handbook* 654. USDA Forest Service, Washington, D.C. USA, pp. 476–488.
- Wenner, N.G., Merrill, W., 1998. Pathological anatomy of needles of *Pinus strobus* exposed to carbon-filtered air or to three times ambient ozone concentrations, or infected by *Canavirgella banfieldii*. *Can. J. Botany-Revue Canadienne De Botanique* 76, 1331–1339.
- White, L.T., 1953. Studies in forest pathology x. decay of white pine in the Timagami Lake and Ottawa Valley areas. *Can. J. Bot.* 31, 175–200.
- Wilhelmi, N.P., Shaw, D.C., Harrington, C.A., St. Clair, J.B., Ganio, L.M., 2017. Climate of seed source affects susceptibility of coastal Douglas-fir to foliage diseases. *Ecosphere* 8 e02011-n/a.
- Woods, A., Coates, K.D., Hamann, A., 2005. Is an unprecedented Dothistroma needle blight epidemic related to climate change? *Bioscience* 55, 761–769.
- Woods, A.J., Martin-Garcia, J., Bulman, L., Vasconcelos, M.W., Boberg, J., La Porta, N., Peredo, H., Vergara, G., Ahumada, R., Brown, A., Diez, J.J., 2016. Dothistroma needle blight, weather and possible climatic triggers for the disease's recent emergence. *Forest Pathol.* 46, 443–452.
- Woods, A.J., Coates, K.D., Watts, M., Foord, V., Holtzman, E.I., 2017. Warning signals of adverse interactions between climate change and native stressors in British Columbia forests. *Forests* 8, 280.
- Wyka, S.A., Broders, K.D., 2016. The new family Septorioideaceae, within the Botryosphaerales and *Septorioidea strobil* as a new species associated with needle defoliation of *Pinus strobus* in the United States. *Fungal Biol.* 120, 1030–1040.
- Wyka, S.A., Smith, C., Munck, I.A., Rock, B.N., Ziniti, B.L., Broders, K., 2017a. Emergence of white pine needle damage in the northeastern United States is associated with changes in pathogen pressure in response to climate change. *Glob. Change Biol.* 23, 394–405.
- Wyka, S.A., McIntire, C.D., Smith, C., Munck, I.A., Rock, B.N., Asbjornsen, H., Broders, K.D., 2017b. Effect of climatic variables on abundance and dispersal of *Lecanosticta acicola* spores and its impact on defoliation on eastern white pine. *Phytopathology*. <http://dx.doi.org/10.1094/PHYTO-02-17-0065-R>.
- Zhao, J.H., Mainwaring, D.B., Maguire, D.A., Kanaskie, A., 2011. Regional and annual trends in Douglas-fir foliage retention: Correlations with climatic variables. *For. Ecol. Manage.* 262, 1872–1886.
- Yeaton, R.I., 1978. Competition and spacing in plant communities: differential mortality of white pine (*Pinus strobus* L.) in a New England woodlot. *Am. Midland Naturalist* 100, 285–293.